

THE EXTERNAL MORPHOLOGY AND PHYLOGENETIC POSITION OF THE WOODLAND CAVE CRICKET (*CEUTHOPHILUS BREVIPES* SCUDDER; ORTHOPTERA; TETTIGONIIDÆ)\*

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INTRODUCTION

The purpose of this paper is to furnish, in one work, the detailed external morphology of an orthopteron which, from an evolutionary standpoint, is among the most primitive of all saltatorial Orthoptera. Although published accounts of portions of the external anatomy have been made available by Drs. Crampton, Walker, and others, no complete morphological study of a native American Rhaphidophorine has been made.

Since Scudder erected the genus *Ceuthophilus* in 1862 more than fifty species have been described. From the point of view of a systematic study of these insects, therefore, it is well to have available a complete account of the morphology of one species to use as a basis for indicating the true relationships of the structures used in the taxonomy of the group.

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Crampton (1923c) has suggested that *Ceuthophilus* may be involved as a carrier of disease organisms. If such should prove to be the case, as appears reasonable, any information regarding the biology and relationships of such a vector may be considered worthy of recording.

Probably the morphology of *Ceuthophilus* is most interesting to the student of insect phylogeny. The close relationships of orthopteroid insects were recognized by Packard (1883) but at that time a careful comparative analysis of the sclerites had not been made. Even earlier, Scudder (1869) had written on the arrangement of the families, but he placed the Gryllidæ and Tettigoniidæ in advance of the Acrididæ because of the greater development of songs, social habits, and the elongate nature of the ovipositor:

Marcovitch (1920) summarized the subject of orthopterous phylogeny and the tree shown by him (Fig. 4) indicates the probable phylogenetic position of the principal groups. The one correction to be made in this tree is that the Tettigoniidæ seem to be directed along the lines of the Acrididæ, with the Gryllids branching in the opposite direction from a point near the base of the Tettigoniids, rather than that the crickets and katydids followed parallel lines apart from the grasshoppers as his tree indicates.

Throughout the present study of *Ceuthophilus* a comparative study of the sclerites has indicated the close relationship of the Grylloblattids, Rhaphidophorines, Gryllacrine, and Stenopelmatines. The crickets clearly have close affinities with the primitive Tettigoniids while such forms as the Tridactylines show qualities in their makeup which indicate an origin in the same stock, but these characters develop further in the higher Tettigoniids and thus lead directly to the grouse-locusts and finally to higher grasshoppers.

The main features of the head and abdominal structures of *Ceuthophilus* have been described by Crampton, Walker, and Yuasa in the papers cited, together with a discussion of evolutionary sequence. The chief original work of this paper is the part dealing with the thoracic sclerites and these are among the most important of all the body structures.

It is hoped that by bringing together the available information on the morphology of this primitive insect a better understanding of its phylogenetic position will result; also that it may aid future taxonomists within the group to locate the structures important in classification.

#### THE HEAD

The head capsule and its appendages do not differ greatly from the corresponding structures of *Stenopelmatus*, which Crampton (1930) has discussed in detail. The head capsule of *Stenopelmatus* in its general features appears rather more broadly rounded in the dorsal area than in the case of *Ceuthophilus*; the antennæ are decidedly more centrally located in *Ceuthophilus*. In these respects *Ceuthophilus* has departed further than *Stenopelmatus* from the primitive type of head capsule represented in *Grylloblatta*. The migration of the eyes toward the vertex points to the higher Tettigoniid type such as *Scudderia*, *Orchelimum*, and *Neoconocephalus* which leads up to the Acrididae. At the other end of the evolutionary scale the eyes are located far down the genæ, as in Isoptera and Dermaptera, which lead to *Grylloblatta*, as discussed by Crampton (1926a, 1932) and Yuasa (1920).

*Head capsule:* As shown in Fig. 3, the dorsal region of the head capsule of *Ceuthophilus* is oval in outline. The *coronal suture cs* is plainly but strongly demarked and terminates in a small triangular spot near the eyes. In this connection the fastigium of the Stenopelmatine *Licodia cerberus* Rehn of Cuba (see Rehn, 1930, Fig. 2) should be mentioned. There are no frontal sutures or epicranial arms in *Ceuthophilus* as there are in *Gryllus*, *Stenopelmatus*, or *Grylloblatta*. The entire region about the eyes and coronal suture is smooth and rather hard. The *parietals par* are the areas on each side of the coronal suture. The areas above the *eyes e* are known as the *temples te*. The *frons f* is just below and between the antennæ while the *genæ ge* are the areas each side above the subgena or *basimandibulare bm*. The latter is a small sclerite which is closely associated with the small *basimandibular membrane bmm*, and lies above the base of the *mandible md*. The margins of the *frontal pits fp*

are somewhat more heavily sclerotized than the surrounding *clypeus c* and *gena*. The frontal pits represent the external openings of the invaginations which form the forward arms of the *tentorium* or *pretentorium pt* shown in Fig. 1.

*Eyes*: The *compound eyes e*, like those of *Stenopelmatus* and *Grylloblatta*, are rather small in comparison to the eyes of most other primitive types of Orthoptera such as Dictyoptera and Gryllidæ. Crampton (1930) has suggested that this reduction of the eyes may be in keeping with the nocturnal habits of these insects (*Ceuthophilus* is nocturnal) and his suggestion is given support by the fact that the eyes of *Gryllotalpa*, which tunnels in soil, are distinctly smaller than those of *Gryllus*, a diurnal surface dweller. The number of facets in each compound eye of *Ceuthophilus* is about three hundred. Ocelli are lacking.

*Antennæ*: The antennæ are long and filiform and vary in number of segments from seventy-five to one hundred and sixty or more in some cases. In some individuals the antennæ are twice the body length. The *antennale an* (Fig. 2) is a delicate ring which bounds the membrane at the base of the *scape sc*. A small projection of the antennale is known as the *antennifer af*. The *scape sc* is the largest segment and rather flat. The *pedicel pd* is short and somewhat bulbous. The next segment, the *post-pedicel ppd*, is considerably longer than the pedicel and assumes the cylindrical form which occurs in the remainder of the antennal segments. The shorter intermediate segments are called *short brachymeres sb* and the more slender ones toward the tip *slender dolichomeres sd*. Additional names have also been applied to the segments in allied Orthoptera because of the differences in size and shape.

*Tentorium*: The inner supporting framework or tentorium of the head capsule of *Ceuthophilus* is formed according to the generalized type discussed by Comstock and Kochi (1902) and Imms (1929, p. 45) in which the chief structures are posterior, anterior, and dorsal arms, and the body of the tentorium. Just as *furcæ* and *apodemes* are invaginations of the external wall of the thorax and abdomen, so the tentorium represents invaginations of the head capsule.

When a potash preparation of the head capsule is studied in



frontal aspect the *anterior arms pt* (Fig. 1) are seen extending backward from the frontal pits where the invaginations occur. The support given to the mandibles which perform the most important work of the appendages of the head may be easily understood. The *dorsal arm st* is a small branch which is attached distally, in *Ceuthophilus*, near the cephalo-mesal margin of the eye. The *posterior arms poc*, resulting from invaginations, the external manifestations of which are the *gular pits gp* near the base of the basicardo, fuse with the anterior arms to form a broad central plate, the body of the tentorium or *eutentorium eu*. The posterior arms are the chief strengthening elements of the margins of the occipital foramen. The *postgenal process pp* bears the *postgenal acetabulum pga* and is separated from the *gena ge* by the *postgenal suture pgs*. The *parastomium psto* is a marginal area extending along the inner ventral edge of the postgenal process.

The commissures connecting the dorsal brain with the suboesophageal ganglion pass through the *neuroforamen nf*, an incision at the bases of the anterior arms. The commissures leading from the suboesophageal ganglion to the prothoracic ganglion pass between the flaring rims of the occipital foramen to the thorax. The semicircular *neuroforamen nf* is probably evolved from the closed structure found in Dictyoptera which leads finally to the entirely fused type exhibited by *Gryllus*. It may be noted that *Grylloblatta*, figured by Walker (1931b), is more like *Gryllus* in this respect than *Ceuthophilus* or *Stenopelmatus*.

*Occipital region:* The *occipital condyles occ* are the points of articulation of the head capsule with the *laterocervicale lc* (Fig. 13). When the external features of the occipital foramen are examined, a flaring band is seen along each side near the gula. This band is the "maxillaria" of Yuasa (1920, p. 262). Dorsad of the condyles the occipital foramen is less heavily sclerotized and the rim is little more than the strengthened margin of the cranium. As Walker (1933, p. 317) states, the occipital suture is not complete at this point.

The *paroccipital tendon pat* and *euoccipital tendon eot* are attached to the rim of the cranium, and the tendons serve as points of attachment for muscles moving the head.

*Clypeus and labrum*: The *clypeus c* is separated from the *frons f* by a well-marked fronto-clypeal suture. The postclypeal and anteclypeal areas are not plainly apparent in *Ceuthophilus*. The outline of the *labrum la* is shown in Fig. 3. The union with the clypeus is strong but allows some movement.

*Mandible*: Fig. 7 shows the insect's right (dextral) mandible as it appears in posterior view. There are three faces and a somewhat triangular base. The *ginglymus gi* is a shallow pit at the base of the frontal face of the mandible. The pit forms an imperfect hook which fits into a niche at the base of the clypeus. The *gnathocondyle* or *hypocondyle h* is a rounded projection which articulates in the *postgenal acetabulum pga* borne on the *postgenal process pp*. The chief tendons which move the mandible on its "rocking" points, the ginglymus and gnathocondyle, are the *flexor ft* which is the heavier of the two because it performs the actual crushing operations of chewing food and the *extensor et* which moves the mandible into an open position. Anyone interested in the powerful muscles extending from the tendons into the head capsule may be guided by the work of Walker (1931b) who has figured in detail the musculature of the head of the allied *Grylloblatta*. The *gnathite gn* is a small sclerite which supplies the attachment of the flexor tendon to the base of the mandible. The *extensor tendon et* is attached directly to the mandible proper at the *epignath* or *extensor prominence ep*. The *gnathapex ga* is a sharp, curved hook for grasping and tearing. The *molar region m* appears as in Fig. 7 and is best adapted for grinding processes. The interior of the mandible is hollow.

*Labium*: The ventral aspect of the labium is shown in Fig. 5. Fig. 4, a dorsal view, shows how the *glossæ gl* arise from the *glossigers gg* near the point where the latter join the *labial stipites li*. The *paraglossæ pg* are also borne by the glossigers. The *palpigers ppg* bear the three-segmented *labial palpi lp*. The *mentum mn* is composed of two regions the posterior of which is more darkly sclerotized. The *gula gu* and *submentum sm* comprise one sclerite, but the former portion is darker colored so that it appears distinct.

The labial structures of *Ceuthophilus* resemble very closely those of *Stenopelmatus* and *Gryllus*.

*Maxilla*: When the ventral surface of the head is examined, the maxilla appears as in Fig. 5. The *stipes s* and the narrow *parastipes ps* are separated internally by a ridge which affords a place of muscle attachment. The *basimaxillary membrane b* bounds the *parastipes ps* laterally. Fig. 6 shows a view of the internal surfaces of the *cardo* which is divided into *basicardo bc* and *disticardo dc*. The point labelled *d* is attached to the postgena near the gular pits and probably functions like a condyle. The *cardo-process cp* is an arm to which the *cardo tendon ctn* is attached. Crampton (1930) describes the manner in which the tendon probably moves the maxilla on the point *d*. The *endocardo ec* is an internal ridge which gives support to the sclerites and offers a place for muscle attachment. The *palpifer pf* is a small sclerite bearing the slender five-segmented *maxillary palpus mp*. The *basigalea bg* is well demarked and bears the *galea g*. The *lacinia l* is toothed as shown in Fig. 5 and is rather strongly sclerotized.

Crampton (1916a, 1923b), Walker (1933), and Yuasa (1920) have discussed in some detail the development of maxillæ in orthopteroid insects. The maxillæ of *Ceuthophilus* are very like those of *Grylloblatta* and *Gryllus*, but differ from those of the Blattidæ on account of the hood-like scoop borne by the galea of the latter. The Decticine genus *Peranabrus* (figured by Crampton, 1923b) shows galea and lacinia somewhat broader than those of *Ceuthophilus*. An examination of specimens of *Conocephalus* and *Neoconocephalus* shows an additional width of the latter appendages which points toward the broad structures found in Acrididæ. With respect to maxillæ, therefore, *Ceuthophilus* exhibits a primitive form.

*Hypopharynx*: The *hypopharynx hp* is a more or less fleshy structure attached to the base of the labium and situated between the labrum and labium as shown in lateral view in Fig. 9. It appears as in Fig. 8 when, with the labrum cut away, it is viewed from above. There are several lobe-like portions of the hypopharynx the apical portion of which is the *distilingua dl*. The *dorsolingua* or *surlingua sl* is the basal portion. The *basilingua bl* is a membrane which forms part of the basal attachment and is the location where the common salivary duct discharges fluid

into the mouth cavity. The oral opening of the oesophagus is near the dorsolingua so that ingested food passes above the hypopharynx. The *lingualora ll* is a small triangular sclerite at the base of the hypopharynx.

*Epipharynx*: The epipharynx is divided into posterior and anterior regions, labelled *poe* and *pre* respectively in Fig. 9. The epipharynx is the roughened inner surface of the labrum and clypeus which is modified to assist in the manipulation of food.

#### THORAX

While investigators have done less work upon the thorax of *Ceuthophilus* than upon the head and abdomen, this region is thought to offer even more valuable clues regarding the phylogenetic position than in the case of the latter. Tegmina and wings are entirely absent. Legs may be reasonably expected to show adaptation to mode of living and so are of scant evolutionary importance. The plates of the neck, pleura and sterna are of the greatest significance and will be discussed as the parts of the thorax are taken up in order.

#### PROTHORAX

*Neck Region*: The *precervicale pre* (Fig. 13) is a small divided plate which is hidden beneath the *pronotum pn*. The important cervical sclerite is the *laterocervicale lc*. Its anterior extremity articulates with the occipital region of the head.

Crampton (1926b, 1933, pp. 140-142) has shown that Blattids, Isoptera, and Mantids are very closely related because of the similarly divided laterocervicale and the mesally extending intercervicale. This latter condition is much different from that exhibited by *Ceuthophilus*. However, Figs. 65, 68, 80, 81, 86, and 94 of Crampton's 1926b paper show that with respect to this sclerite *Ceuthophilus* is a primitive member of the Saltatoria. It is similar to *Gryllacris* but most like *Grylloblatta*. Among the Gryllids, *Tridactylus* has an undivided laterocervicale which is directed mesally similarly to that of roaches. *Gryllus* has a partially divided sclerite which comes nearer *Ceuthophilus* in form, while *Oecanthus* is very like *Ceuthophilus* except for the division of the sclerite. Apparently the condition in *Oecanthus* leads to that occurring in *Tettix* and other Acridids.



*Pronotum:* The *pronotum pn* of *Ceuthophilus* completely covers the *episternum es*<sub>1</sub> and *epimeron em*<sub>1</sub>, but as Duporte (1919) has indicated, this is the result of the growing over of the pronotum rather than the forcing out of the pleural sclerites. The pronotum is smooth and polished. A like condition prevails in *Gryllacris* but in the related *Stenopelmatus* the beginnings of pronotal sulci are visible and in the remaining subfamilies of Tettigoniidae both the presence of sulci and the form of the pronotum point toward the condition found in Acrididae. The effect of wing muscles is of course entirely absent in *Ceuthophilus*. The pronotum of *Grylloblatta* does not extend ventrally so as to completely cover the pleural sclerites but is more like that of Dermaptera. Neither does the Gryllid pronotum show consistent similarities to that of *Ceuthophilus*. The pronotum of *Gryllotalpa* and *Tridactylus* is not very different from the *Ceuthophilus*-like forms but that of *Gryllus* is more flattened dorsally and that of *Oeconthus* is more suggestive of *Grylloblatta* or even of a Mantid. With respect to the pronotum, therefore, it appears that *Ceuthophilus* stands near the base of the whole Tettigoniid line leading directly to the Acrididæ while the Gryllids represent an offshoot, possibly from a point near *Stenopelmatus*. It should be noted that although the Gryllids are an offshoot from the stem which leads to the Acrididæ, they may exhibit qualities which constitute examples of development inherited from primitive Tettigoniids. Any such inheritance is interesting because certain of the same qualities were developed in the main Tettigoniid line leading to the Acrididæ.

*Propleuron:* The *episternum es*<sub>1</sub> of *Ceuthophilus* is somewhat striking in appearance because of the bilobed condition. At the base it is fused with the *precoxale pr* and is closely affixed to the base of the *pronotum pn*.

The *epimeron em*<sub>1</sub> is a narrow curved sclerite at the base of which there is a tapering prolongation toward the *spiracle sp*. The *episternum es*<sub>1</sub> and *epimeron em*<sub>1</sub> are separated externally by the pleural suture and a narrow fold projects inwardly to form the *endopleuron* or *lateral apodeme*. This serves for the attachment of muscles and one-third of its length from the base an *apophysis apop* is attached which extends to it from the *furcasternum fs*.



The *trochantin tr* is a narrow sclerite between the base of the *coxa cx* and the *precoxale pr*.

*Prosternum*: The *presternum* has entirely disappeared in *Ceuthophilus*. The *basisternum bs* is fused with the *precoxale pr* and is present as a narrow transverse sclerite. The *furcasternum fs* is shaped like the *basisternum* and, as shown in Fig. 13, bears the *apophyses apop* which extend internally to the *endopleuron* already mentioned. The *spinasternum ss* is represented externally only by a small crescent-shaped sclerite in the midst of membrane. Internally, a small four-armed spine of the *spinasternum* is present, the anterior arms of which are each weakly forked again.

It is difficult to make a phylogenetic evaluation of the propleural and prosternal sclerites of *Ceuthophilus* upon a basis of present information. The chief available papers are those of Crampton (1926b), Duporte (1919), and Voss (1905). *Grylloblatta*, *Gryllus*, *Periplaneta*, and other forms have been figured, but in some cases the sclerites hidden by the overlapping pronotum have not been shown. A study of several Tettigoniid genera would be very helpful.

The roach represents a rather complex condition as compared to *Ceuthophilus*. The existence of both *precoxale* and *antecoxale*, the division of the *trochantin*, the frequent division of the *precoxale* and its separation from the *basisternum*, and the large size and frequent union of the sternal elements are characteristic of roaches.

A condition contrasted to that of the roach is found in the grasshopper *Disosteira* (see Crampton, 1918c; Duporte, 1919). The *episternum* and *epimeron* are reduced to narrow, tapering sclerites. A basal spur of the *epimeron* extends posteriorly as in *Ceuthophilus*. The pleural suture is vertical. The elements of the *prosternum* are united to form a triangular sclerite connected laterally to the *episternum*.

The condition exhibited in *Ceuthophilus* is intermediate between these two extremes, but distinctly nearer *Dissosteira*. *Grylloblatta* is both roach-like and grasshopper-like in these respects. The condition of the *prosternum* of *Gryllus*, *Gryllobtalpa* and *Tridactylus* indicates a transition to the grasshopper-like condition from a condition much like that of *Ceuthophilus*.

*Leg:* The outline and proportions of the fore leg are shown in Fig. 10. The *coxa* articulates with the base of the pleuron and the chief muscles concerned in allied species are discussed by Duporte (1919). The *coxa cx* is somewhat elongate and is grooved to receive the conical *trochanter tch* which articulates with it. Fig. 26 shows the mesal surface of the *coxa cx* and the *tendons ten* which pull the *trochanter tch*.

The *femur fe* is firmly joined to the *trochanter tch* and little movement is possible. The femur is grooved beneath and unarmed except for a single small spur near the apex on the inner side of the groove.

The *tibia ti* is cylindrical and of uniform diameter. It is armed with a pair of small apical spurs dorsally and four pairs of similar spurs ventrally.

The four-segmented *tarsus ta* is loosely articulated and in lateral view appears as in Fig. 10. The first, which may result from the fusion of two segments, and fourth segments are longest. The ventral surfaces of the tarsal segments are membranous and slightly dilated to form a pad-like or pulvilli-form condition.

Fig. 11 shows the chief structures important to the articulation of the claws or unguis. The *unguis ung* is curved, slender and unarmed. It articulates with the dorsal apical margin of the *distitarsus ta<sub>4</sub>* and is moved by the action of the *tendon ten* which pulls the *retractile plate rp*. There is no *arolium*. These structures compose the *pretarsus* of de Meijere (1901, p. 423) and are similar on the other two legs. The pretarsi of several Orthoptera, including *Ceuthophilus*, have been figured and discussed by Holway (1935).

The legs are variable in Orthoptera on account of different living habits and so are difficult to interpret from an evolutionary standpoint. However, the very large bilobed pads of the Japanese *Galloisiana* (see Caudell and King, 1924) and the distinctly bilobed pads on the third tarsal segment of *Scudderia* and allied genera may have some relation to the slightly dilated condition in *Ceuthophilus*. In general, the fore leg of *Ceuthophilus* is much like that of *Grylloblatta*. The number of tarsal segments does not seem to be important since in the Rhaphidophorine *Daihinia* the tarsi do not all have the same number of segments (see Caudell, 1916, p. 685).

## MESOTHORAX

*Mesonotum*: The *mesonotum mnn* of *Ceuthophilus* is narrower and slightly deeper than the *pronotum pn* but does not otherwise differ materially from it. The complete absence of tegmina and wings accounts for the chief differences between meso- and metanotum of *Ceuthophilus* and those of most Saltatoria. *Grylloblatta* does not show so much growth of the notum ventrally and neither does *Stenopelmatus*, but the nymph of *Melanoplus* (see Snodgrass, 1909, Fig. 55) is very like *Ceuthophilus*, showing that characteristics of *Ceuthophilus* persist in the ontogeny of such more highly evolved species.

*Mesopleuron*: A large part of the *episternum es<sub>2</sub>* is exposed below the overhanging *mesonotum mnn*. This sclerite is roughly triangular, is curved anteriorly, and has a prominent prolongation in the direction of the atrophied precoxale. There is a lengthwise suture as shown in Fig. 13.

The *epimeron em<sub>2</sub>* is largely concealed, but occurs as a narrow, curved sclerite beside the episternum. The cephalad portion extends beyond the *endopleural suture* as the *endopleuron* and is long and curved at the base. A smaller external hook is present at the caudal-ventral extremity.

The *trochantin tr* is a narrow crescent-shaped sclerite.

*Mesosternum*: The *basisternum bs* and *furcasternum fs* form a single broad transverse plate. The furcal pits mark the position of the internal *furcæ fur* each arm of which is unequally bifurcate while a median spina extends posteriorly and has two curved "horns" on either side. The *spinasternum ss* is a narrow sclerite which is not connected to the furcasternum.

As in the case of the prothorax, the pleuron and sternum of the mesothorax are considerably different from those of a roach. The pleural suture of *Grylloblatta* (Crampton, 1915) is slightly more horizontal than in the case of *Ceuthophilus* and the laterosternite is probably fused to the episternum in the case of the latter. In respect to the propleuron *Gryllus* (Duporte, 1919, Fig. 13) is much like *Ceuthophilus*, but the prothoracic epimeron is wider. Among the higher Tettigoniids the presence of wings brings about a change of shape and a specialization for articulation of wing ossicles. As Snodgrass (1909, pp. 537, 557, Figs. 43,

55, 56, 57, 70, 71) has brought out, the short-winged Decticine *Anabrus* has essentially the same form of pleuron as in adult Acrididæ although nymphal Acrididæ are not yet specialized for flight and so show a more primitive condition. A pleural ridge in the episternum of *Ceuthophilus* persists in Acridids.

The broad united *furca*- and *basisternum fs bs* of *Ceuthophilus* is intermediate between the very broad condition of *Dissosteira* and the broadly lobed condition of *Grylloblatta*. The *furca*-sternum and *basisternum* of the roach are more separated than in *Ceuthophilus* and so in respect to the mesosternum *Ceuthophilus* occupies a position near *Grylloblatta* and annectent to Acridids.

*Leg*: The *coxa cx* is shaped as shown in Fig. 16 and is grooved above. The *trochantin tr* is an important articulatory sclerite. A mesal view of the *coxa cx* and *trochanter tch* is shown in Fig. 22. The trochanter is freely jointed with the coxa but the joint with the *femur fe* is only slightly moveable. The latter is grooved beneath and armed with two small spurs, one apical spur on the mesal surface and the other externally on the ventral margin near the apex. The *tibia ti* is slender, cylindrical, curved at the base, armed with three small dorsal spurs in an irregular line, three pairs of ventral spurs and two pairs of apical spurs of which the ventral pair is the longer. The four-segmented *tarsus ta* with *ungues ung* does not differ materially from the prothoracic tarsus.

#### METATHORAX

*Metanotum*: The *metanotum mtn* is attached to the *mesonotum mn* by a fold of membrane and in life the anterior margin lies below the posterior border of the latter. The metanotum is longer and not so deep as the mesonotum.

*Metapleuron*: The *episternum es<sub>3</sub>* is roughly triangular in shape and a pleural ridge extends from the base nearly the entire length. It is very much like the *mesepisternum es<sub>2</sub>* except that the prolongation corresponding to the laterosternite of allied species is lacking.

The *epimeron em<sub>3</sub>* is likewise similar to the *mesepimeron em<sub>2</sub>* but the *endopleural apodeme* at the base is not so long as in the latter.



The *trochanter tr* is narrow and curved.

*Metasternum*: The *basisternum bs* and *furcasternum fs* form a semi-quadrate sclerite which is deeply cleft anteriorly. The *furca fur* are curved arms which are tri-furcate.

As Snodgrass (1909, p. 556) has stated, "Meso- and meta-pleura closely resemble each other" in Orthoptera. In general, the pleural sclerites of both segments show the same tendencies and a comparison of figures in the references cited leads to almost identical conclusions.

*Leg*: The posterior leg is shown in Fig. 14. The *coxa cx* is marked by a longitudinal scar externally. Mesally (Fig. 21) the coxa is divided by a median line into an anterior and posterior area. The *trochanter tch* is largely concealed as seen from an external aspect and the relationships are better shown in Figs. 21 and 15. The trochanter is composed of a wide basal rim and the trochanter proper. The articulatory process *X* is connected with the coxa and the *tendon ten* moves the trochanter. The trochanter fits over a small neck-like process of the *femur fe* and the femur and trochanter move as a unit just as in the non-jumping legs.

The *femur fe* is greatly enlarged basally to accommodate the huge muscles which move the *tibia ti*. The femur is deeply sulcate beneath and both lower margins bear small spines. The apex of the femur is modified to receive the base of the *tibia ti* which is shown in Fig. 18. The articulatory processes *X*, *X* and the two *tendons ten*, the lower of which flexes the leg while the upper one performs the action of leaping, illustrate the manner in which simple mechanical processes are utilized by these insects. Blatchley (1920, p. 20) states that the ventral apical lobes of the femur prevent the tibia from wobbling in leaping.

The *tibia ti* is slender and sulcate above. The margins of the groove are lined with small spines and there are five pairs of spurs which are slightly staggered. The three pairs of apical spurs are figured. The number of ventral spurs is variable. Usually there is one very small spur near the apex, but in some cases there is an additional pair nearby. The two hind tibiae of the same individual may differ in this respect. Fig. 12 shows a section of tibia with a *spur spu* removed to give a view of the *spur calyx spu c* in which it is set.



The four-segmented *tarsus ta* is very like that of the other body segments.

The form of the hind femora and tarsi is very variable in the genus *Ceuthophilus* and allied genera. Caudell (1916) has figured some of the forms important to classification.

#### ABDOMEN

The anatomy of the abdomen of *Ceuthophilus* is reasonably familiar to students of comparative morphology, due largely to the researches of Chopard, Crampton, and Walker in the papers listed. The terminal segments of each sex exhibit interesting features from the standpoint of a comparative study and will be discussed separately.

*Abdominal segments:* The abdomen of *Ceuthophilus* is sub-cylindrical in general appearance. Crampton (1933) has pointed out that in this respect *Grylloblatta* (which is much like *Ceuthophilus*) is more closely allied to primitive saltatorial Orthoptera than to roaches in which the abdomen is strongly flattened. Staining is necessary to show the exact extent of the sclerites. As shown in Fig. 19, the tergites  $t_{1-10}$  are separated by pleural membrane from the sternites  $s_{1-9}$ . A similar condition occurs in the Grylloblattids, *Stenopelmatus*, *Camptonotus* and, as far as the writer knows, among all higher Tettigoniids also. The tergites of *Oecanthus*, too, grade into pleural membrane, but *Gryllus domesticus* L. shows well-defined sclerites and a distinct area of membrane. In *Gryllotalpa* the membrane is somewhat folded and *Tridactylus* shows a condition in which the sternites and membrane overlap the tergites. In the Acrididæ, however, the opposite condition, in which the tergites have grown over the lateral margins of the sternites, is found.

Under a compound microscope the pleural membrane of *Ceuthophilus* shows many, small spines, most of which bear a seta at the base, and some occur on the tergites. It is interesting to note that these and the dorsal spines of *Pristoceuthophilus tuberculatus*, described by Caudell (1916, Fig. 15), may be homologous with those of *Galloisiana* mentioned by Caudell and King (1924, p. 54).

*Spiracles:* The abdominal spiracles of *Ceuthophilus* are eight

pairs in number and are located as shown in Figs. 13 and 19. The seven posterior abdominal spiracles are somewhat smaller than those of the thorax and first abdominal segment. Each spiracular opening is guarded by two small elongate sclerites. The structures of the spiracles have not been examined in detail here, but are described in the work of Vinal (1919) on *Dissosteira*.

The location of the spiracles of *Ceuthophilus* seems to be a primitive condition among Saltatoria. In all local Acrididæ except the Acrydiinæ the abdominal spiracles are borne by the margins of the tergites. As an example of the grouse-locusts, *Acrydium* has only the eighth spiracle present on the tergite. In *Gryllus*, *Gryllotalpa*, and *Oecanthus*, as in the Tettigoniids, all occur in the membrane, but in *Ripipteryx*, from Central and South America, the eighth is borne by the tergite and thus the latter and *Acrydium* are intermediate between the Tettigoniids and higher Acrididæ.

Among the Dictyoptera the spiracles of roaches (see Crampton, 1925) are borne by small sclerites known as subtergites or pleurites, while *Stagmomantis* has the spiracles on the tergites. The exact lines of evolution represented by the different positions of the spiracles are not well understood, but probably the subtergites are portions of the tergites. The subtergites are lost in Tettigoniids, but in the Acrididæ the tergites extend laterally and surround the spiracles.

#### TERMINAL STRUCTURES OF MALE

*Tergites:* The tergites slowly decrease in length toward the apex of the abdomen, but the ninth  $t_9$  is the first to be decidedly smaller than those anterior to it. The dorsal margin of the eighth tergite  $t_8$  shows a variety of specific variations within the genus and is utilized by systematists on this account. In *C. brevipes* sc. this margin is smoothly convex and scarcely rises above the level of the other tergites, but in other species it is emarginate, raised in the form of a crescent, or may be distinctly truncate. The ninth tergite  $t_9$  is slightly shorter dorsally than at the lateral extremities. It is sometimes practically concealed by the eighth tergite, depending upon the degree of extension of the intertergal membrane. The tenth tergite  $t_{10}$  is a very narrow sclerite which is frequently hidden by the ninth.

*Sternites*: The ninth sternite  $s_9$  differs from the other ventral sclerites in being modified as the subgenital plate. As shown in Fig. 19, it is partially divided near the base. An important feature of the subgenital plate is the apical membrane, which is in the form of curved "horns"  $ms_9$ , and which is used as a specific character in systematic work. The beginning student should not confuse these "horns" with the membranous, horn-like arms of the penis which are called parameres.

In the primitive *Grylloblatta* the ninth sternite bears a pair of coxites and the latter in turn styli. It may be that the posterior portion of the ninth sternite of *Ceuthophilus* represents the coxite and that the membranous "horns" are degenerate styli. According to Blatchley (1920, p. 602), the subgenital plate of the Gryllacrinae is deeply notched transversely and bears short obtuse styli. Karny (1934) has discussed and figured styli in both sexes of very small nymphs of *Rhaphidophora* sp. from eastern Asia. In higher Tettigoniids, such as *Neoconocephalus* and *Scudderia*, a transverse division of the sternite is not as apparent but styli are present. Gryllids bear no styli. Walker (1922, Fig. 58) has interpreted the structures of Tettigidea to include coxites and in higher Acrididae they are represented by the apex of the subgenital plate. With respect to the ninth sternite, therefore, *Ceuthophilus* shows a primitive condition.

*Cercus*: The *cercus ce* of the adult is slender, tapers to a fine point, and is non-segmented. As shown in Fig. 23, the apical portion has small irregular areas of heavier sclerotization which suggest segmentation but actual segments are not demarked. The cercus of the first instar nymph appears as in Fig. 20. Although difficult to see, three small segments are present. The basipodite or *basicercus bas* at the base of the cercus is shown in Fig. 25. In some specimens the two sclerites are imperfectly divided.

The cylindrical eight-segmented cerci of *Grylloblatta* and the nine-segmented appendages of *Galloisiana* are more like Plecoptera than the sub-triangular cerci of roaches. As noted above, the cerci of *Ceuthophilus* show affinities with a multi-articulate adult condition, and in *Pristoceuthophilus cercalis* (see Caudell, 1916, Fig. 17) five small segments are present. *Diestrammena*

and most Gryllids (the cerci of *Tridactylus* are two-segmented) possess very long, tapering, non-segmented cerci, but those of *Stenopelmatus* are slightly stouter and shorter than *Ceuthophilus* and may point toward the short, broad types of most higher Tettigoniids. A comparison of *Ceuthophilus nodulosus* (see Caudell, 1916, Fig. 10) with *Amblycorypha* or *Scudderia*, and *Pristoceuthophilus celatus* (l. c., Fig. 13) with *Conocephalus* shows two types of cerci in the more advanced subfamilies of Tettigoniidæ which apparently are presaged in the more primitive Rhaphidophorinæ. The broad, often blunt cerci of Acrididæ are well known as their modifications, especially in *Melanoplus*, are used in classification.

*Supra-anal plate:* The *supra-anal plate sa* is a sub-triangular flap, the apex of which extends above the anus. It is most heavily sclerotized at the margins and about a central depression. Hubbell (1934, p. 223) refers to a basal portion, the epiproct, and a smaller deflexed distal portion, the suranale. While these terms are in accepted systematic use, the term epiproct in a strict morphological sense applies to the tenth tergite, as it was so used by Crampton (1929, 1933, p. 151).

The supra-anal plate is characteristic of nearly all Saltatoria, though absent in roaches and mantids, and frequently is absent in Plecoptera. Hebard (1916, Figs. 14-16) has figured a small chitinous hook on each side of the supra-anal plate of the adult male *Stenopelmatus*. In many Gryllids and higher Tettigoniids the supra-anal plate is fused with the tenth tergite and in some Gryllids the line of fusion may be seen. The transverse line of demarcation is conspicuous in many Acrididæ, especially in nymphs as Walker (1922, p. 21) has stated. The paired arms, *fureulea*, of *Melanoplus* are borne by the tenth tergite.

*Paraprocts:* The *paraprocts pa* (Figs. 25 and 27) are narrow sclerites which give support to the membrane ventrad of the supra-anal plate and between the cerci. They are variously known as laminae subanales and podical and parapodial plates. The drawings are made from stained potash preparations, but in the natural state each paraproct appears as a roughly triangular area. The paraprocts of *Grylloblatta* are similarly weakly sclerotized and though stronger in other Tettigoniids and crickets they



are seldom conspicuous as in *Ripipteryx* and *Tridactylus*. In Acrididæ they have undergone no great change of form except that heavier sclerotization has brought about broad flat plates.

*Pseudosternite*: The *pseudosternite pst* is a heavily sclerotized hood-like structure just anterior to the penis. It is supported laterally by *rami ra* and by endopophyses which extend inward from the arch *ar* which covers the ejaculatory duct leading to the penis. The postcornua or dorsal lobes *pc* are folds of the lower margin laterad of the arch. The roof of the pseudosternite is nearly flat in *C. brevipes* Sc., but is sharply gable-like in certain species; the arch, postcornua and rami are also subject to specific variation.

Walker (1922, pp. 24-28) has pointed out that, unlike the Rhabdiphorinæ, the higher subfamilies of Tettigoniidæ do not possess a well developed pseudosternite. Neither is it present in roaches and *Grylloblatta*, but it is prominent in most crickets and in *Gryllus* resembles that of *Ceuthophilus* which suggests that the crickets may have evolved from the lower groups of Tettigoniids. The pseudosternite of the Gryllids, especially in the case of *Oecanthus* (see Walker, l. c., fig. 46), shows a tendency to be nearer the penis than in *Ceuthophilus* and this also holds true in *Acrydium*. The pseudosternite of higher Acridids is well developed, resembles that of *Ceuthophilus*, and is valuable in systematic work.

*Penis*: The penis of *Ceuthophilus* is largely membranous, although the *ventral lobe lop* is strengthened and spinulose. The *parameres pm*, which are latero-anterior arms, and the lightly sclerotized area between them frequently are invaginated while in a resting condition and so are examined with difficulty. The ventral lobe is also partly invaginated at times and Walker (1922, pp. 24-28) has discussed the formation of a "spermatophore sac" preparatory to the extrusion of the spermatophore and its attachment to the female.

In order to appreciate the critical features of the female genitalia one must know something of the functions performed. Turner (1916) has outlined in general the breeding habits of the different families of Orthoptera and the question as to whether the sexual products are inclosed in a spermatophore is readily



seen to be important. The latter says that spermatozoa are transferred directly in Acrididæ, and so the strong pointed structures described in detail by Walker (l. c.) and Hubbell (1932) would appear useful. However, Uvarov (1928, pp. 53-56) describes spermatophores found in grasshoppers; they are apparently very small.\* Fulton (1931, pp. 227-231, Figs. 4 and 5) has described the structure of the spermatophore in *Nemobius* and Henneguy (1904, pp. 267-268, Figs. 272 and 273) has discussed the spermatophores of various groups and has given figures in the case of *Gryllus*. The parameres are heavily sclerotized in many higher Tettigoniids and may point toward the condition in Acrididæ; the long endapophyses of *Ceuthophilus* also seem to persist in the more advanced forms.

#### TERMINAL STRUCTURES OF FEMALE

*General features:* The eighth, ninth and tenth tergites  $t_{8-10}$  (Fig. 24) differ rather markedly in shape from the respective sclerites of the male. The eighth sternite  $s_8$ , which serves as a shield at the base of the lower valves  $vv$ , shows modifications in the direction of the egg guides of Acrididæ. The cercus, paraprocts and supra-anal plate are similar in both sexes. The important structures are those relating to the ovipositor and since they have been carefully described and figured by Crampton (1929) and Walker (1919b) in papers that are readily accessible, only the main features will be mentioned here.

The genital aperture opens between the eighth and ninth sterna into the inner valves  $iv$  which are completely inclosed by the larger dorsal valves  $dv$  and ventral valves  $vv$ .

*Ventral valves:* At the base of each ventral valve  $vv$  is the *basivalvula*  $bsv$  which is partly concealed by the eighth sternite  $s_8$ . A small triangular sclerite representing a part of the ninth sternum, the valvifer  $vf$ , serves as a point of attachment for both ventral and dorsal valves. Each ventral valve has a decided inner fold along the ventral margin and a narrow fold along the upper margin. The four apical teeth appear as figured.

\* An important paper by Mr. R. E. Snodgrass, "The Abdominal Mechanisms of a Grasshopper," (Smithsonian Misc. Coll. 94, 6, 1-99, 41 Figs., 1935) has recently appeared which includes a review of the knowledge of fertilization in Acrididæ.

The ventral valve is attached at the base to the basivalvula and by a slim ramus to the valvifer *vf*.

*Dorsal valves*: The dorsal valves are equal in length to the ventral valves and when the valves are closed overlap the upper margins of the latter. Near the inner ventral margin of the dorsal valve is a distinct sclerotized projection which may be called the *inner hook ih*. The superior apophysis *sap* is a subtriangular sclerite firmly attached to the base of the valve *dv* and the anterior point extends within the distal tergites as a point of attachment for tendons.

*Inner valves*: The inner valves *iv* are about two-thirds the length of the other valves and are held within the dorsal valves by the inner hooks *ih*. There are folds near the ventral margins of the inner valves and dorsally the two valves are joined as shown by Walker (1919b, Fig. 3). The ramus *rm* is a short bar at the base of each inner valve which extends within the body as a point of attachment.

Fig. 17 shows a ventral view of the developing ovipositor of a small female nymph. The left ventral valve, belonging to the eighth sternite *s<sub>8</sub>*, is cut away to better show the dorsal and inner valves developing from the ninth sternite. Practically a parallel condition prevails in *Stenopelmatus* and has been figured by Walker (1919b, 1919a) in *Conocephalus* and *Grylloblatta*. In the first of the two papers cited the latter author has presented a splendid series of figures and a thorough discussion of the types of ovipositors exhibited by the several Orthopteroid families. The advanced form shown by higher Tettigoniids has been discussed; also the differences exhibited by crickets and the way *Ripipteryx* and Acrydiinæ are primitive to higher Acrididæ.

#### PARTIAL BIBLIOGRAPHY

- ANDER, K. 1933. Ueber *Anisoura nicobarica* m., eine bemerkenswerte Laubheuschrecke aus der Familie Gryllacrididæ. *Konowia*, 12, 217-230, 11 figs.
- BAUMGARTNER, W. J. 1911. Observations on the Gryllidæ, IV, Copulation. *Paris Univ. Sci. Bull.*, 5, 307-319.
- BERLESE, A. 1882. Ricerche sugli organi genitali degli Ortoteri. *Atti della R. Acad. dei Lincei*, 3a serie, 11, 42 pp., 2 pls.
- BLATCHLEY, W. S. 1920. *Orthoptera of Northeastern America*. The Nat. Pub. Co., Indianapolis, Ind., 784 pp., 246 figs.

- BOLDYREV, B. H. 1915. Contributions a l'etude de la structure des spermatophores et des particularities de la copulation chez Locustodea et Grylloidea. Petrograd Horae soc. ent. ross., 41, 6, 1-245, ill.
- BRUNNER VON WATTENWYL, C. 1876. Die morphologische Bedeutung der Segmente, speziell des Hinterleibes bei den Orthopteren. Festschr. zool.-bot. Ges. Wien, 1-18, 3 pls.
- CARPENTIER, F. 1923. Musculature et squelette chitineux chez les Orthopteres. Mem. Acad. Roy. Brussels, (2), 7, fsc. 3, 1-56, 11 figs.
- CAUDELL, A. N. 1916. The genera of the Tettiginiid insects of the subfamily Rhaphidiphorinae found in America north of Mexico. Proc. U. S. Nat. Mus., 49, 655-690, 28 figs.
- . 1923. Grylloblatta in California. Can. Ent., 55, 148-150.
- . 1924a. Notes on Grylloblatta with description of a new species. Jour. Wash. Acad. Sci., 14, 369-371.
- . 1924b. Change of a preoccupied generic name. Proc. Ent. Soc. Wash., 26, 4, p. 92.
- CAUDELL, A. N., AND KING, J. L. 1924. A new genus and species of the notopterous family Grylloblattidae from Japan. Proc. Ent. Soc. Wash., 26, 53-60, 1 pl.
- CHANG, K. F. 1931. The external anatomy of *Oedalus marmoratus* Thunb. Pt. I. External anatomy of the head and mouthparts. J. St. John's Sci. Soc., 1, 15-38. (Abstract in Lingnan Sci. J., 12, p. 152.)
- CHIU, S. F. 1933. A preliminary study of the Gryllotalpinae of Canton. Pt. I. External morphology. Lingnan Sci. Jour., 12, 547-554, 5 pls.
- CHOPARD, L. 1918. Note preliminaire sur la conformation de l'organ copulateur des Orthopteres. Bull. Soc. Zool. de France, 43, 59-67.
- CHOPARD, L. 1920. Recherches sur la conformation et le developpement des derniers sgments abdominaux chez les Orthopteres. Insecta Rennes, 10, 1-112. (Sep. pag.)
- . 1921. Recherches . . . (Cont.). Insecta Rennes, 11, 113-224. (Sep. pag.)
- . 1922. Recherches . . . (Cont.). Insecta Rennes, 12, 225-352, 7 pls., 14 figs. (Sep. pag.)
- COMSTOCK, J. H. 1930. An Introduction to Entomology. The Comstock Pub. Co., Ithaca, N. Y., 230-269, 70 figs.
- COMSTOCK, J. A., AND KOCHI, C. 1902. The skeleton of the head of insects. Amer. Nat., 36, 13-45, 29 figs.
- CRAMPTON, G. C. 1915. The thoracic sclerites and systematic position of *Grylloblatta campodeiformis* Walker, a remarkable annectent "Orthopteroid" insect. Ent. News, 26, 337-350, 1 pl.
- . 1916a. A comparative study of the maxillae of the Acrididae (Oedipodinae and Tettigininae), Phasmidae and Phyllidae. Psyche, 23, 3, 83-87, 1 pl.
- . 1916b. The lines of descent of the lower Pterygotan insects, with notes on the relationships of the other forms. Ent. News, 27, 244-258, 297-307, 1 fig.

- . 1917a. A comparison of the antennæ of the Grylloblattids and Embiidæ, to demonstrate the relationship of these two groups of insects. *Can. Ent.*, 49, 213-217, 2 figs.
- . 1917b. A phylogenetic study of the lateral head, neck and prothoracic regions in some Apterygota and lower Pterygota. *Ent. News*, 28, 398-412, 1 pl.
- . 1917c. A phylogenetic study of the terminal abdominal segments and appendages in some female Apterygotan and lower Pterygotan insects. *Jour. N. Y. Ent. Soc.*, 25, 4, 225-237, 2 pls.
- . 1918a. A phylogenetic study of the terga and wing bases in Embiids, Plecoptera, Dermaptera and Coleoptera. *Psyche*, 25, 1, 4-12, 1 pl.
- . 1918b. A phylogenetic study of the terminal abdominal structures and genitalia of male Apterygota, Ephemeroptera, Odonata, Plecoptera, Neuroptera, Orthoptera, and their allies. *Bull. Brklyn. Ent. Soc.*, 13, 7, 49-68, 6 pls.
- . 1918c. The thoracic sclerites of the grasshopper, *Dissosteira carolina* L. *Ann. Ent. Soc. Amer.*, 11, 4, 347-368, 3 figs.
- . 1919a. Notes on the phylogeny of the Orthoptera. *Ent. News*, 30, 42-48, 64-72, 1 fig.
- . 1920a. The terminal abdominal structures of the primitive Australian termite *Mastotermes darwinensis* Froggatt. *Trans. Ent. Soc. Lond.*, 1920, 137-145, 1 pl.
- . 1920b. Notes on the lines of descent of the lower winged insects. *Psyche*, 27, 116-127, 6 figs.
- . 1921a. The origin and homologies of the so-called superlinguæ or paraglossæ (paragnaths) of insects and related Arthropods. *Psyche*, 28, 84-92, 1 pl.
- . 1921b. The sclerites of the head, and the mouthparts of certain immature and adult insects. *Ann. Ent. Soc. Amer.*, 14, 2, 65-103, 7 pls.
- . 1923a. A comparison of the terminal abdominal structures of an adult alate female of the primitive termite, *Mastotermes darwinensis*, with those of the roach, *Periplaneta americana*. *Bull. Brklyn. Ent. Soc.*, 18, 85-93, 1 pl.
- . 1923b. A phylogenetic comparison of the maxillæ throughout the orders of insects. *Jour. N. Y. Ent. Soc.*, 31, 77-106, 6 pls.
- . 1923c. The cave cricket, *Ceuthophilus*, as a possible vector of pathogenic organisms. *Jour. Ec. Ent.*, 16, p. 46.
- . 1925. The external anatomy of the head and abdomen of the roach, *Periplaneta americana*. *Psyche*, 32, 195-220, 3 pls.
- . 1926a. The affinities of *Grylloblatta* indicated by a study of the head and its appendages. *Psyche*, 33, 78-84, 4 figs.
- . 1926b. A comparison of the neck and prothoracic sclerites throughout the orders of insects from the standpoint of phylogeny. *Trans. Amer. Ent. Soc.*, 52, 199-248, 8 pls.

- . 1927a. The thoracic sclerites and wing bases of the roach, *Periplaneta americana*, and basal structures of the wings of insects. *Psyche*, 60-72, 3 pls.
- . 1927b. The abdominal structures of the Orthopteroid family Grylloblattidæ and the relationships of the group. *Pan Pacific Ent.*, 3, 115-135.
- . 1928a. The eulabium, mentum, submentum, and gular region of insects. *Pomona Jour. Ent. and Zool.*, 20, 1-18, 3 pls.
- . 1928b. The grouping of the insect orders and their lines of descent. *The Entomologist*, 61, 82-85, 1 pl.
- . 1928c. Anatomical evidence that *Cylindracheta* is a Gryllo-talpoid, not an Embiid. *Ent. Mitteilungen*, 17, 252-257, 1 pl.
- . 1929. The terminal abdominal structures of female insects compared throughout the orders from the standpoint of phylogeny. *Jour. N. Y. Ent. Soc.*, 37, 453-496, 8 pls.
- . 1930. The head structures of the Orthopteran *Stenopel-matus*—a contribution to the study of the external anatomy of *Stenopel-matus*. *Pan Pacific Ent.*, 6, 97-110, 2 pls.
- . 1931. A phylogenetic study of the posterior metathoracic and basal abdominal structures of insects, with particular reference to the Holometabola. *Jour. N. Y. Ent. Soc.*, 39, 323-357, 5 pls.
- . 1932. A phylogenetic study of the head capsule in certain Orthopteroid, Psocoid, Hemipteroid and Holometabolous insects. *Bull. Brklyn. Ent. Soc.*, 27, 19-55, 5 pls.
- . 1933. The affinities of the archaic Orthopteroid family Grylloblattidæ, and its position in the general phylogenetic scheme. *Jour. N. Y. Ent. Soc.*, 41, 127-166.
- . 1935. A defense of the view that the Grylloblattids are descended from the protorthoptera and lead to the Tettigonioid family Stenopelmatidæ—a reply to Dr. E. M. Walker. *Jour. N. Y. Ent. Soc.*, 43, 97-111.
- DEMEJERE, J. C. H. 1901. Ueber das letzte Glied der Beine bei den Arthropoden. *Zool. Jahrb., Anat.* 14, 417-476, 8 pls.
- DEWITZ, H. 1875. Ueber Bau und Entwicklung des Stachels und Legescheide einiger Hymenopteren und des grünen Heuschrecke. *Zeit. wiss. Zool.*, 25, 174-200, 2 pls.
- DUPORTE, E. M. 1919. The propleura and the pronotal sulci of the Orthoptera. *Can. Ent.*, 51, 147-153, 13 figs.
- FORD, N. 1923. A comparative study of the abdominal musculature of Orthopteroid insects. *Trans. Canad. Inst.*, 14, 207-319, 17 pls.
- . 1926. On the behavior of *Grylloblatta*. *Can. Ent.*, 58, 66-70, 1 fig.
- FULTON, B. B. 1931. A study of the genus *Nemobius*. *Ann. Ent. Soc. Amer.*, 24, 205-237, 5 figs.
- GERHARDT, U. 1913. Copulation und Spermatophoren von Grylliden und Locustiden. *Zool. Jahrb., syst.*, 415-532, 2 pls.



- . 1921. Neue Studien über Copulation und Spermatophoren von Grylliden und Locustiden. *Acta Zool.*, Stockholm, 2, 293-327, 4 figs.
- GRABER, V. 1870. Die Aehnlichkeit in im baue der Ausserlichen weiblichen Geschlechtsorgane bei den Locustiden und Agridien auf Grund ihrer Entwicklungsgeschichte. *Sitzber. der K. Akad. d. wiss. Wie.*, 61, 597-616, 1 pl.
- . 1889. Ueber den Bau und die phylogenetische Bedeutung der embryonalen Bauchanhänge der Insekten. *Biol. Centralbl.*, 9, 355-363.
- HANDLIRSCH, A. Zur Phylogenie der Hexapoden (Vorlauf. Mitt.). *Wien. Sitzungsab. Mathem. Naturw. Classe*, 112, Abth., 1, 716-738, 1 pl.
- . 1909. Die fossilen Insekten und die Phylogenie der rezenten Formen. Leipzig, Wilhelm Engelmann, 1x-1430, 51 pls.
- . 1925. Geschichte, Literatur, Technik, Palaontologie, Phylogenie und Systematik der Insekten. *Schroder's Handbuch der Entomologie*, Jena. Band., 3, 1201 pp., 1040 figs.
- HEBARD, MORGAN. 1916. A study of the species of the genus *Stenopelmatus* found in the United States. *Jour. N. Y. Ent. Soc.*, 24, 70-86, 16 figs.
- HENNEGUY, L. F. 1904. *Les Insectes. Morphologie-Reproduction-Embryogenie*. Paris, Masson and Cie, 804 pp., 4 pls., 622 figs.
- HOKE, GLADYS. 1924. The anatomy of the head and mouthparts of the Plecoptera. *Jour. Morph.*, 38, 347-373, 6 pls.
- HOLWAY, R. T. 1935. Preliminary note on the structure of the pretarsus and its possible phylogenetic significance. *Psyche*, 42, 1, 1-24, 3 pls.
- HSU, Y. 1931. Morphology, anatomy and ethology of *Gryllus mitratus* Burm. *Lingnan Sci. J.*, 10, 187-216, 5 pls.
- HUBBELL, T. H. 1932. A revision of the Puer Group of the North American genus *Melanoplus*, with remarks on the taxonomic value of the concealed male genitalia in the Cyrtacanthacrinæ. *U. of Mich. Mus. Zool. Misc. Pub.*, 23, 1-64, 4 figs.
- . 1934. Treatment on Rhaphidophorinæ, 220-243 in: Hebard's *Dermoptera and Orthoptera of Illinois*. *Ill. Nat. Hist. Sur. Bull.*, 20, Art. III.
- IMMS, A. D. 1926. The biology and affinities of *Grylloblatta*. *Proc. Ent. Soc. Lond.*, 1, p. 57, 1 photograph.
- . 1927. On the affinities of the Grylloblattidæ. *Psyche*, 34, 36-39.
- . 1929. *A General Textbook of Entomology*. Methuen and Co., Ltd., xii and 698 pp., 607 figs.
- . 1931. *Recent Advances in Entomology*. Blakiston's Son and Co., Philadelphia, 1-89.
- KARNY, H. H. 1925. Die Methoden der phylogenetischen Forschung in: *Abderhalden Handbuch der biol. Arbeitsmethoden*, Abt., IX, Teil 3, 211-500, 40 figs.
- . 1930a. Phylogenetische und tiergeographische Erwägungen zur Systematik der Rhaphidophorinen. *Arch. klass. phylogen. Ent.*, 1, 57-76, 1 map, 9 figs.

- . 1930b. Zur Systematik der Orthopteroiden Insekten. Zweiter Teil. *Treubia*, Buitenzorg, 12, 431-461.
- . 1934. Zur Kenntnis der ostasiatischen Rhabdiphorinen (Orth. Salt. Gryllacrididæ). *Konowia*, 13, 70-80, 1 fig.
- LEE, M. O. 1925. On the mechanism of respiration in certain Orthoptera. *J. Exper. Zool.*, 41, 125-154, 2 figs.
- LESPEDES, C. 1855a. Memoire sur le Spermatophores des Grillons. *Ann. Sci. Nat.*, 4 serie, 3, 366-377, 1 pl.
- . 1855b. Deuxieme not sur les Spermatophores du *Gryllus sylvestris*. *Ann. des Sci. Nat.*, 4 serie, 4, 244-249, 1 pl.
- LU, H. T., AND CHEN, T. T. 1928. The anatomy of *Crytaacanthacris flavicornis*. *Proc. Nat. Hist. Soc.*, Fukien Christian University, Foochow, 1, 49-58, 2 pls.
- MARCOVITCH, S. 1920. Grasshoppers of Tennessee. *Tenn. State Board of Ent. Bull.* 33, 9, 2, 1-111, 32 figs.
- MARTIN, J. F. 1916. The thoracic and cervical sclerites of insects. *Ann. Ent. Soc. Amer.*, 9, 35-83, 15 figs.
- MORSE, A. P. 1920. Manual of the Orthoptera of New England. *Proc. Bost. Soc. Nat. Hist.*, 35, 6, 197-556, 20 pls.
- NEL, R. I. 1929. Studies on the development of the genitalia and the genital ducts in insects. I. Female of Orthoptera and Dermaptera. *Quart. Jour. Mic. Sci.*, 73, 25-85.
- NEWELL, A. G. 1918. The comparative morphology of the genitalia of insects. *Ann. Ent. Soc. Amer.*, 11, 109-142, 14 pls.
- NUSBAUM, J. 1882. Zur Entwicklungsgeschichte der Ausführungsgänge der Sexualdrüsen bei den Insecten. *Zool. Anz.*, 5, 637-643.
- PACKARD, A. S. 1883. The systematic position of the Orthoptera in relation to other orders of insects. Third Rep. U. S. Ent. Commission, Wash., 281-345, 40 pls.
- PANTEL, J. 1915. Notes orthopterologiques, VI Le "vomer sous-anal" n'est pas le "titillateur"; etude des segments abdominaux et principalement du segment terminal des male chez les Phasmides. *Ann. Soc. Ent. France*, (1915), 173-233, 4 pls.
- PEYTOUREAU, A. 1893a. Recherches sur l'anatomie et le developpement de l'armure genitale male des Insectes Orthopteres. *Comp. Rend. Ac. Sc.*, 117, 293-295.
- . 1893b. Recherches sur l'anatomie et le developpement de l'armure genitale femelle des Insectes Orthopteres. *Comp. Rend. Ac. Sc.*, 117, 749-751.
- . 1895. Remarques sur l'organisation, l'anatomie comparee et le developpement des derniers segments du corps des Insectes Orthopteres. These Bordeaux, 248 pp., 22 pls.
- REHN, J. A. G. 1930. On certain tropical American genera of Stenopelmatinae, with descriptions of two new West Indian species. *Trans. Amer. Ent. Soc.*, 56, 363-373, 4 figs.
- SAUSSURE, H. DE, AND ZEHNTNER, LEO. 1894. Notice morphologique sur les Gryllotalpiens. *Rev. Suisse de Zool.*, fasc. 2, 403-430, 2 pls.

- SCUDDER, S. H. 1869. The arrangement of the families of Orthoptera. Proc. Bost. Soc. Nat. Hist., 12, 226-235.
- SILVESTRI, F. 1927. Contribuzioni alla conoscenza dei Grylloblattidæ. Bollett. Lab. Zool. Scuola sup. agr., Portici, 20, 107-121, 8 figs.
- . 1931. Notes on *Grylloblatta campodeiformis* and a description of a new variety. Trans. Amer. Ent. Soc., 57, 291-295, 5 figs.
- SNODGRASS, R. E. 1907. A comparative study of the thorax in Orthoptera, Euplexoptera and Coleoptera. Proc. Ent. Soc. Wash., 9, 95-108, 27 figs.
- . 1909. The thorax of insects and the articulation of the wings. Proc. U. S. Nat. Mus., 36, 511-595, 30 pls.
- . 1927. Morphology and mechanism of the insect thorax. Smiths. Misc. Coll., 1, 1-108, 44 figs.
- . 1928. Morphology and evolution of the insect head and its appendages. Smiths. Misc. Coll., 81, 3, 158 pp., 57 figs.
- . 1929. The thoracic mechanism of a grasshopper and its antecedents. Smiths. Misc. Coll., 82, 111 pp., 54 figs.
- TURNER, C. L. 1916. Breeding habits of the Orthoptera. Ann. Ent. Soc. Amer., 9, 2, 117-135.
- UVAROV, B. P. 1928. Locusts and Grasshoppers. William Clowes and Sons, Ltd., Lond., 352 pp., ill.
- VINAL, S. C. 1919. The respiratory system of the Carolina Locust. (*Disosteia carolina* Linne). Jour. N. Y. Ent. Soc., 27, 19-22, 16 figs.
- VOSS, F. 1905. Ueber den thorax von *Gryllus domesticus*. Zeit. wiss. Zool., 78, 268-521, 645-759, 3 pls.
- WALKER, E. M. 1914. A new species of Orthoptera, forming a new genus and family. Can. Ent., 46, 93-99, 7 figs.
- . 1919a. On the male and immature state of *Grylloblatta campodeiformis* Walker. Can. Ent., 51, 131-139, 13 figs.
- . 1919b. The terminal abdominal structures of orthopteroid insects: a phylogenetic study. Pt. I. Ann. Ent. Soc. Amer., 12, 267-316, 71 figs.
- . 1922. The terminal structures of orthopteroid insects: a phylogenetic study. Pt. II. Ann. Ent. Soc. Amer., 15, 1-89, 106 figs.
- . 1931a. On the clypeus and labrum of primitive insects. Can. Ent., 63, 75-81, 1 pl.
- . 1931b. On the anatomy of *Grylloblatta campodeiformis* Walker. 1. Exoskeleton and musculature of the head. Ann. Ent. Soc. Amer., 24, 519-536.
- . 1932. Prognathism and hypognathism in orthopteroid insects. Can. Ent., 64, 223-229, 1 pl.
- . 1933. On the anatomy of *Grylloblatta campodeiformis* Walker. 2. Comparisons of head with those of other orthopteroid insects. Ann. Ent. Soc. Amer., 26, 309-344, 41 figs.
- YUASA, HACHIRO. 1920. The anatomy of the head and mouthparts of Orthoptera and Euplexoptera. Jour. Morph., 33, 2, 251-287, 163 figs.

## ABBREVIATIONS

af	antennifer	gi	ginglymus
an	antennale	gl	glossa
apop	apophysis	gn	gnathite
ar	areh of pseudosternite	gp	gular pits
b	basimaxillary membrane	gu	gula
bas	basipodite	h	gnathocondyle or hypocondyle
bc	basicardo	hp	hypopharynx
bg	basigalea	ih	inner hook of dorsal valve
bl	basilingua	im	intervalvular membrane
bm	basimandibulare	iv	inner valve
bmm	basimandibular membrane	l	lacinia
bs	basisternum	la	labrum
bsv	basivalvula	lc	laterocervicale
c	clypeus	li	labial stipites
cds	cardosuture	ll	lingualora
ce	cercus	lop	ventral lobe of penis
cp	cardoprocess	lp	labial palpus
cs	coronal suture	m	mola
ctn	cardotendon	md	mandible
ex	coxa	mn	mentum
d	articulatory process of basi- cardo	mn	mesonotum
dc	disticardo	mp	maxillary palpus
dl	distilingua	m s <sub>9</sub>	membraneous "horns" of 9th sternite
dv	dorsal valve	mtn	metanotum
e	compound eye	nf	neuroforamen or neural in- cision
ec	endocardo	occ	occipital condyle
em	epimeron	p	tentorial arch or trabecula
ep	epignath or extensor promi- nence	pa	paraproct
eot	euoccipital tendon	par	parietal
es	episternum	pat	paroccipital process
et	extensor tendon	pe	postcornua or dorsal lobes of pseudosternite
eu	eutentorium or body of ten- torium	pd	pedicel
f	frons	pf	palpifer
fe	femur	pg	paraglossa
fp	frontal pits or clefts	pga	postgenal acetabulum
fs	furcasternum	pge	postgena
ft	flexor tendon	pgs	postgenal suture
fur	furca	pl	postlingua or "linguaten- don"
g	galea	pm	paramere
ga	gnathapex		
ge	gena		
gg	glossiger (Basiglossa)		



pn	pronotum	sc	scape
po	pons valvularum	sd	slender dolichomeres of antenna
poc	parocciput or posterior arms	sl	dorsolingua
poe	postepipharynx	sm	submentum
pp	postgenal process	sp	spiracle
ppd	postpedicel	spn	spine
ppg	palpiger	spu	spur
pr	precoxale	spu c	spur calyx
pre	precervicale	ss	spinasternum
pre	pre-epipharynx	st	supratentorium
ps	parastipes	t <sub>1</sub>	tergites of abdomen
pst	pseudosternite	ta	tarsus
psto	parastomium	tch	trochanter
pt	pretentorium	te	temples
ra	ramus of pseudosternite	ten	tendon
rm	rami of inner valvulæ	ti	tibia
rp	retractile plate	tr	trochantin of coxa
s	stipes	ung	ungues or claws
s <sub>1</sub>	sternites of abdomen	vf	valvifer
sa	supra-anal plate	vv	ventral valve
sap	superior apophysis	X, X,	furcal points
sb	short brachymeres of antenna		

## CEUTHOPHILUS BREVIPES

## PLATE VII

- Figure 1. Anterior view of tentorium and neighboring parts.  
Figure 2. Antenna.  
Figure 3. Frontal view of head.  
Figure 4. Anterior view of glossae and paraglossæ.  
Figure 5. Posterior view of back of head.  
Figure 6. Inner surface of cardo and stipes.  
Figure 7. Posterior view of dextral mandible.  
Figure 8. Anterior view of hypopharynx.  
Figure 9. Lateral view of hypopharynx and upper and lower lip, with most of head capsule removed.

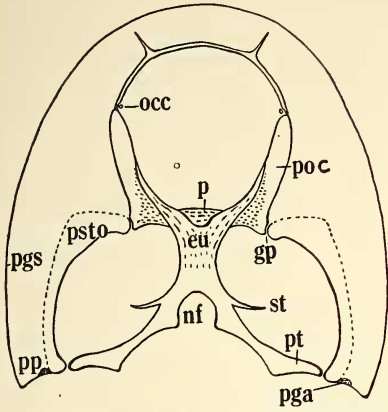


Fig. 1

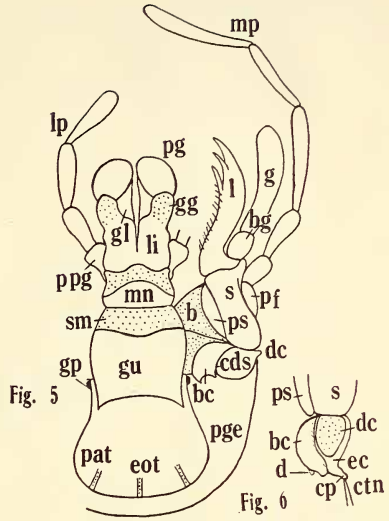


Fig. 5

Fig. 6

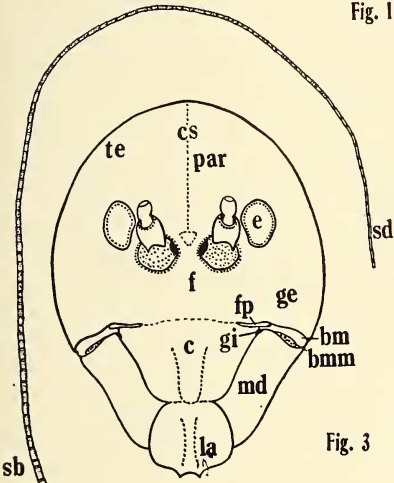


Fig. 3

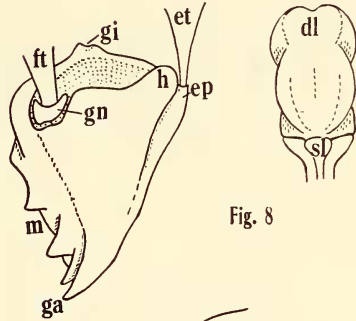


Fig. 7

Fig. 8

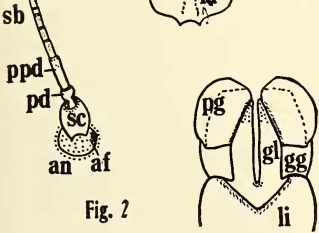


Fig. 2

Fig. 4

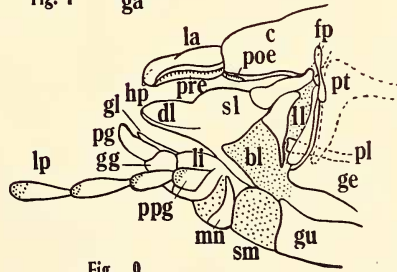


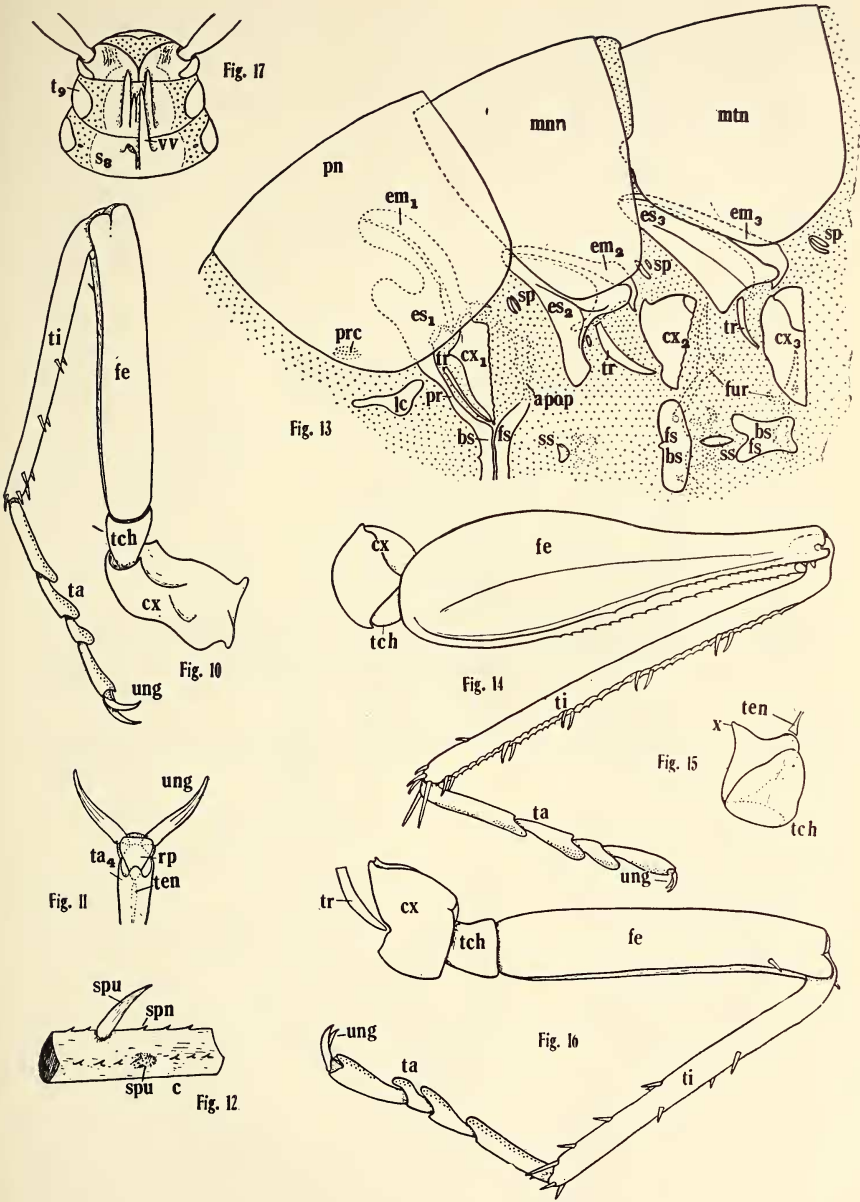
Fig. 9

## CEUTHOPHILUS BREVIPES

## PLATE VIII

- Figure 10. Lateral view of fore leg.  
Figure 11. Ventral view of pretarsus of fore leg.  
Figure 12. Section of tibia of rear leg.  
Figure 13. Lateral view of thoracic sclerites.  
Figure 14. Lateral view of rear leg.  
Figure 15. Mesal aspect of rear trochanter.  
Figure 16. Lateral view of mesothoracic leg.  
Figure 17. Ventral view of terminal abdominal segments of small nymphal female.





## CEUTHOPHILUS BREVIPES

## PLATE IX

- Figure 18. Lateral view of base of rear tibia.  
Figure 19. Lateral view of abdomen of male.  
Figure 20. Apex of cercus of small nymph.  
Figure 21. Mesal aspect of base of rear leg.  
Figure 22. Mesal aspect of base of mesothoracic leg.  
Figure 23. Apex of cercus of adult.  
Figure 24. Lateral view of terminal abdominal segments of adult female.  
Figure 25. Latero-posterior view of region about base of cercus in adult male.  
Figure 26. Mesal aspect of base of fore leg.  
Figure 27. Dorso-posterior view of terminal abdominal structure of adult male.

